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Behavioral Interactions Among Individuals in Territorial...

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Behavioral interactions among individuals in territorial clusters of the longfin damselfish *Stegastes diencaeus.*

by

Anna Melina Ludlow

A Thesis

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7 May 1996
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ABSTRACT

In this study, I examined the presence of a dear enemy effect in territorial clusters of a permanently territorial fish. Longfin damselfish (Stegastes diencaeus) often form territorial clusters in which individual fish defend contiguous territories. I examined the pattern of interactions between individuals in ten such clusters. Fish often crossed territorial borders and intruded into other territories. Most intrusions occurred among neighbors and in most cases these intrusions were tolerated. Fish within clusters seemed to show a dear enemy effect; individuals were less aggressive towards territorial neighbors. However, interactions did not occur randomly within the cluster; some fish intruded and/or received more intrusions than others. A social structure may exist within a cluster determining access to territories.

INTRODUCTION

The purpose of this study was to examine the presence of a dear enemy effect in territorial clusters of the longfin damselfish Stegastes diencaeus. Damselfish have long been studied for their territorial behavior (Low, 1971; Myrberg, 1972; Myrberg and Thresher, 1974; Thresher, 1976; Ebersole, 1977; Mahoney, 1981; Kohda,1981; Katzir, 1981; Bartels, 1984; Itzkowitz, 1990). Most coral reef species are highly aggressive and defend all-year territories from which they obtain food, shelter and oviposition sites (Itzkowitz, 1977). Such behavior often results in an exclusive area for the defender and thus a certain degree of spatial isolation from other conspecifics. However it is common among some damselfish species to form territorial clusters in which several individuals aggregate and defend contiguous territories (Itzkowitz, 1978; Bartels, 1984). These clusters may result from the partitioning of a limited habitat (Itzkowitz, 1977), or may arise as a social phenomenon where individuals seem to prefer to be part of a cluster (Itzkowitz, 1978). In other species of fish, individuals obtain advantages from clustering in terms of brood defense (Gross and MacMillan, 1981).

Territorial neighbors in a cluster are often less aggressive to each other than to non-neighbors. This has been termed the dear.enemy effect (Fisher, 1954). According to this hypothesis, once territorial boundaries have been established, a neighbor poses little threat to a territory owner, and aggressive behavior is correspondly reduced. Neighbor discrimination results from individual recognition, and prevents escalated fights between neighbors (Jaeger, 1981; Ydenberg et al., 1988). However, most studies on the dear-enemy effect were examined on seasonally territorial individuals (see Ydenberg et al, 1988 for a review). As yet, This phenomenon has not been described in permanently territorial species.

In permanently territorial animals, clustering implies that territorial neighbors will spend considerable time in close proximity, and such neighbors will be present longer than among seasonally territorial animals. I anticipate that the dear enemy effect would be even more likely to occur in these clusters.

In this study, I examined the pattern of individual interactions in territorial clusters of the permanently territorial longfin damselfish Stegastes diencaeus. I predicted that three social arrangements could exist in territorial clusters among permanently territorial animals: (1) territorial neighbors would be less aggressive to each other as a result of the dear enemy effect and boundaries between neighbors be respected; (2): no dear enemy effect would exist; individuals often cross territorial boundaries and show considerable aggressive interactions; and (3): a dear enemy effect exist but would apply only to some neighbors, with more aggression directed at some individuals but not others. This latter case has some support, as in colonies of other territorial damselfish species (Myrberg, 1972; Itzkowitz, 1978) a social structure resembling a dominance hierarchy has been found (Myrberg, 1972; Itzkowitz, 1978). However, these studies did not examined the interactions among individuals in relation to territorial boundaries.

METHODS

This study was conducted at the marine laboratory of the National University of Mexico in Puerto Morelos Q. Roo, located in the Mexican Caribbean coast (86, 52' W, 26¡, 52' N), from October 1994 to January 1995. The study site was located in the back reef. The habitat consisted primarily of coral heads separated by sand and sea grass. The coral heads were composed of mixed live and dead coral with algae and other small invertebrates forming a covering mat. The water depth varied from approximately 1.5 m near the reef to 2m near the lagoon.

Selection of clusters and estimates of individual territory size.

A territorial cluster was defined as two or more fish defending contiguous territories on a discrete coral head. These were separated from each other by at least 1.5m of sand. The alternative condition, which is as common as the clusters, was a coral head occupied only by a single fish. Ten clusters were selected on the back reef. The number of individuals in a cluster varied from 3 to 14. Cluster sites were identified with a numbered ribbon attached to the coral head. Once all cluster sites were tagged, individual territories were mapped in each cluster. Estimates of territory size were made for each fish using the following measurements: 1. The locations where feeding took place without being chased by any other fish in the cluster and; 2. the location at which an intruder was chased. These measures were taken during a 10 minute observation period for each fish.

Data collection

Observations were made during the day from 10 AM to 3PM, times for

which patterns of activity are relatively stable (Aguirre, et al, unpublished data). In order to avoid a possible bias from observations of different clusters taken over different months, all clusters were observed throughout the three-month period. Individual fish from different clusters were observed in one day, so that individual observations for all clusters took place at the same time.

Once territory sizes were estimated for all individual fish in the cluster (after the 10 minute observations), each fish in the cluster was observed once individually for 15 minutes. During these observations the following data were collected: 1. Number of neighbors: A neighbor was defined as a fish whose territory could be entered by swimming in a straight line without crossing another territory. Individuals were also considered neighbors if their territorial borders were separated by non-defended space, with the distance between the border smaller than the diameter of the largest of the two territories. 2. The number of intrusions the fish made into another territory. There could be 3 outcomes of these intrusions: i) the intruder was not chased by the territory holder, in which case the behavior of the intruder within the territory was also recorded (whether it nipped in the territory or not); ii) the intruder was chased out of the territory, and iii) the intruder was chased by the defender but it would chase back and the interaction escalated into a fight. 3. The number of border fights between neighbors. These fights occurred at territorial borders where it was unclear which fish initiated it. 4. Frequency of nips of the substrate performed in the territory. 5. The number of chases of intruders from outside the cluster.

Once each individual fish was observed, the entire cluster was observed for an additional 15 minutes. During these observations, any interaction between individuals in the cluster was recorded.

In clusters of 8 or less, all individuals were observed. In larger clusters a minimum of 7 individuals were observed. A total of 64 fish were observed over a period of three months.

Tagging

In order to determine whether individuals remained in their territories during the observation period, two individuals from each cluster were selected randomly and removed for tagging. Fish were tagged by injecting acrylic non-toxic paint under the scales. After being released (about 1m away from their territory), all tagged fish returned to their territories. The tags lasted for approximately 6 weeks.

Sex determination

Most species in the genus Stegastes have no clear sexual dimorphism. The longfin damselfish is no exception, and differentiation between the sexes without dissection was not possible. At the end of the study, 16 randomly selected fish from the 10 clusters and four solitary fish (not in clusters) were dissected for sex determination .

Analysis

The data for interactions was analyzed by constructing sociometric matrices for each cluster (Boyd and Silk, 1983). Matrices were constructed with all interactions together as shown in table 2. A social structure in each cluster would be defined by the distribution of these interactions. A chi squared test was applied to the matrix to test for randomness. In this case, the test consisted of a contingency table and residual analysis . Spearman rank correlations and Kruskal-Wallis ANOVA tests were used to test specific questions about the pattern of intrusions within each cluster. Data from all the clusters (N=64) were used for the analyses.

RESULTS

Interactions

Fish residing in clusters often crossed territorial boundaries of other fish in that cluster (Table 1).
Most intrusions occurred among neighbors. From a total of 323 intrusions observed in all clusters, 297 (91.95%) were performed by neighbors. Only 26 intrusions (8.05%) were performed by non-neighbors.

Larger clusters typically had a larger number of fish defending territories. Given more territories within a cluster, fish were likely to have more neighbors. Indeed, a significant correlation was found between cluster size and number of neighbors (r_s= .41, p<.01, n=64). Consequently, individuals with more neighbors may be expected to engage in more intrusions. However, fish with more neighbors did not seem more inclined to intrude on their neighbor s territories (r_s=.22, p>.05, n=64), but they were more likely to receive more intrusions (r_s= .40, p<.01, n=64).

Despite the considerable number of intrusions, only in16% of these was the intruder chased out of the territory. This proportion was significantly smaller than the 50% that would be expected by chance (Binomial test z= -12.46, p<.001, n=64). Intrusions from non-neighbors were rare, but when they occurred,non-neighboring intruders were chased 76.92% of the time;

The results from the sociometric matrices showed that individuals do not randomly intrude into other territories. Table 2 shows an example of a matrix for one of the clusters. Table 3 shows, with the chi-squared values for the matrices, that territorial intrusions towards neighbors were nonrandomly distributed in 7 out of 10 clusters. This finding means that: 1) some individuals in the clusters intruded upon more territories and/or received more intrusions than others, and 2) for some fish in the cluster, the number of intrusions received was significantly different from the number of intrusions performed. Table 4 gives a summary of the individual fish in each cluster that showed significant differences in the number of intrusions performed versus intrusions received. These values were obtained from the sociometric matrices.

Several reasons could account for the differences beween individuals within the cluster in the number of intrusions received and performed. One hypothesis is that individual differences in the number of intrusions performed was related to differences in aggression. I compared the number of intrusions performed by all fish in the cluster with different agonistic behaviors. I found that fish that intruded upon more territories were more likely to win more fights ($r_s = .30$, $p < .05$, $n = 64$).

Another possibility is that a social structure existed within each cluster resulting in differential access to territories among the fish. Dominance hierarchies within the clusters were difficult to construct because of the overall low levels of aggression observed. I was able to construct hierarchies in only three clusters using fights. Therefore, in order to test for the presence of a social structure, individual fish in all clusters were ranked a-priori using four different behaviors: 1.- Number of intrusions performed; the fish that performed most intrusions was assigned the highest rank, 2.- Number of intrusions received; the fish that received less intrusions was assigned the highest rank, 3.- Number of chases performed when being intruded; the fish that chased most was assigned the highest rank, and, 4.- Number of chases received; the fish that was chased least was assigned the highest rank. Hierarchies were constructed with these four criteria and compared using a Friedman analysis of variance by ranks. The test showed that hierarchies were not significantly different for each cluster (see table 5); that is, the ranks obtained by each different ranking system are concordant with each other.

Sex determination and feeding behavior.

Althouugh feeding while intruding other territories was uncommon (10.21 % of total intrusions in all clusters), it seemed to be a possible reason for intruding upon other territories. Individuals that performed more feeding nips in their own territory, also received more feeding nips from their intruders (r_s=.256, $p<.05$, N=64, Fig 3). However, the total number of nips observed in a cluster was not significantly different between clusters (Kruskal-Wallis test=9.0, p=.437).

Dissections showed that 10 out of 20 individuals had non-differentiated gonads and sex could not be determined. Of the remaining 10, 5 were males and 5, females. Of these, two males and one female were solitary fish (not from the clusters). Courtship behavior was observed during the 3-month study period only in clusters that were not part of my study.

DISCUSSION

Territorial clusters of the permanently territorial longfin damselfish S. diencaeus , seem to show a dear enemy effect. The dear enemy hypothesis predicted that territorial neighbors would show reduced aggression among them. This notion was supported in this study since territory holders show a very low degree of aggressive responses towards intruders. Most territorial intrusions occurred among neighbors and were tolerated. However, intrusions from non-neighbors in the same cluster were not tolerated; non-neighboring intruders were chased most of the time. The small number of fights observed in the clusters also supports the dear enemy hypothesis.

This high tolerance for neighbor intrusions is particularly striking considering the highly aggressive behavior of other damselfish species towards conspecifics (Myrberg and Tresher,1974). In the longfin damselfish, territory owners in a cluster will vigorously attack a non-familiar intruder placed in their territory (inside a bottle, pers. obs). Although intrusions from conspecifics outside the cluster were very rare, when they occurred, one or more individuals in the cluster would be highly aggressive towards the intruding fish (pers. obs).

A social structure seemed to exist among the fish in the clusters determining access to territories. The most aggressive individuals seemed to have access to more territories without being chased by the defender. Intrusions did not occur randomly among the fish in the cluster. Some individuals initiated a large number of intrusions while receiving very few and some received many intrusions but initiated few or none. Also, some territories were intruded by more than one fish while others where intruded consistently by one single fish. In the former case, some of these intruders were chased and some were not. Therefore, not all fish had equal freedom in crossing territorial boundaries. Furthermore, some individuals intruded into a territory without being chased but would respond aggressively to an intrusion from such territory holder.

Such behavioral differences within clusters may simply be the result of individual differences in aggression (i.e. individuals that intrude more are more aggressive). The fact that fish that intruded more territories won more fights seems to support this idea. However, there seemed to be a pattern such that the fish that intruded more territories also received less intrusions, chased more fish when being intruded, and, received less chases when intruding other territories.

Why individuals enter other territories is unclear. Feeding can be a reason for entering upon other territories. In a heterogeneous habitat (which is the case for these clusters), food may have been unevenly distributed; some territories may have more food resources than others. The number of intrusions in which nipping behavior occurred was correlated to the number of nips performed by the defender in its territory. Thus, intruders may have been lured by the rich food found in their neighbor s territory. It is also possible that the nipping behavior of the defender caused the intruder to also nip. For example, nipping behavior in some coral-reef fish has been found to attract other fish to the food source (Itzkowitz, 1980).

The presence of a dear enemy effect in these territorial clusters has the consequence of territorial boundaries existing for some individuals (non-neighbors) but not for others (neighbors). This finding has significant consequences for the concept of intraspecific aggression in territorial behavior of damselfish. Damselfish can differentiate between intruders from different species and show species-specific attack distances which result in the presence of variable territorial borders (Myrberg and Tresher, 1974; Harrington and Losey, 1990; Itzkowitz, 1990). One of these territorial borders is usually defined for conspecific intruders. In this study however, some individuals were tolerated in any part of the defender s territory, whereas others were chased out from the same location. Moreover, territorial boundaries seemed to be variable for the same conspecific intruders; that is, the intruder might be chased at one time and not at other times.

In summary, fish in territorial clusters often crossed territorial borders and have considerable interactions with each other. This seems to be consistent with the dear enemy hypothesis since most of these intrusions occurred among neighbors and were highly tolerated; most intruders were not chased and there was a very low frequency of agonistic encounters. The few intrusions that occurred among non-neighbors were not tolerated. However, intrusions did not occur randomly among territorial neighbors; some individuals received more intrusions than others and some individuals were more likely to intrude than others. A social structure seems to exist in the clusters determining access to territories. This would involve some degree of individual recognition among the fish.

cluster	n /cluster	intrusions/ cluster	median intrusions/ individual
1	8	75	2
2	3	12	1
3	7	46	3
4	7	23	2
5	6	47	4
6	5	24	3
7	5	20	2
8	7	30	2
9	9	24	1
10	7	27	1

Table 1. Total number of intrusions observed for all individuals in each cluster. The second column denotes the number of individuals present in the cluster except clusters 9 and 10 in which the numbers denote the number of individuals observed in the cluster. The third column is the number of intrusions observed per cluster and the fourth column is the median number of intrusions per individual in that cluster.

ind	1	2	3	4	5	6	7	8	sent	rec
1	-	0	2	0	8	0	0	0	10	2
2	2	-	0	0	13	0	0	0	15	3
3	0	0	-	0	19	0	1	0	20	8
4	0	0	3	-	1	0	0	0	4	4
5	0	0	2	1	-	6	0	0	9	43
6	0	0	0	0	1	-	0	0	1	11
7	0	0	1	0	1	5	-	0	7	1
8	0	3	0	3	0	0	0	-	6	0

Table 2. Matrix of intrusions for cluster 1. The first column and the top row represent the individual fish in the cluster. The first column denotes the fish intruding and the top row the receiver of such intrusions.The numbers in each row denote the frequency of intrusions to each territory. The last two columns denote the total number of intrusions performed and received respectively, for the individual fish in that row. The chi-squared test consisted on a contingency table and residual analysis.

ind	1	2	3	4	5	6	7	8	sent	rec
1	-	0	2	0	8	0	0	0	10	2
2	2	-	0	0	13	0	0	0	15	3
3	0	0	-	0	19	0	1	0	20	8
4	0	0	3	-	1	0	0	0	4	4
5	0	0	2	1	-	6	0	0	9	43
6	0	0	0	0	1	-	0	0	1	11
7	0	0	1	0	1	5	-	0	7	1
8	0	3	0	3	0	0	0	-	6	0

Table 2. Matrix of intrusions for cluster 1. The first column and the top row represent the individual fish in the cluster. The first column denotes the fish intruding and the top row the receiver of such intrusions.The numbers in each row denote the frequency of intrusions to each territory. The last two columns denote the total number of intrusions performed and received respectively, for the individual fish in that row. The chi-squared test consisted on a contingency table and residual analysis.

cluster	n/cluster	chi-square	p
1	8	59.54	p<.001*
2	3	15.56	p<.001*
3	7	23.12	p<.001*
4	7	6.46	p>.05
5	6	28.33	p<.001*
6	5	20.85	p<.001*
7	5	10.03	p<.05*
8	7	33.80	p<.001*
9	9	6.81	p>.05
10	7	6.72	p>.05

Table 3. Chi-square values for the sociometric matrices of intrusions.

cluster	n/cluster	# of individuals with significant values
1	8	4
2	3	2
3	7	2
4	7	1
5	6	4
6	5	1
7	5	1
8	7	3
9	9	0
10	7	0

Table 4. Number of fish per cluster for which the chi-squared values of the contingency table analyses in the matrices were significant. For such fish, the total number of intrusions performed and intrusions received are: one significantly smaller and one significantly larger than expected by random.

cluster	n/cluster	Friedman test	p
1	8	.86	.83
2	3	-	-
3	7	.94	.81
4	7	.12	.98
5	6	1.25	.74
6	5	.06	.99
7	5	-	-
8	7	1.32	.72
9	9	.2	.97
10	7	.13	.98

Table 5. Values for the Friedman analysis of variance by ranks for each cluster. Non-significant values indicate that ranks for each fish are consistent among the different hierarchies. The test was not applied to clusters 2 and 7 because no chases were observed in these clusters and therefore no ranks could be assigned with this criteria (chases performed and chases received).

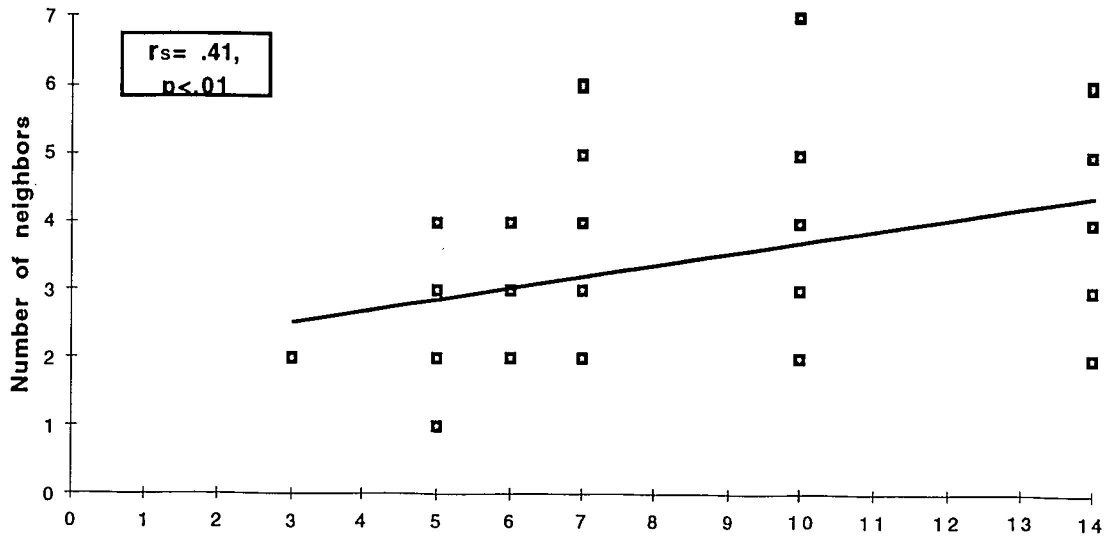

Fig 1. Ranges of possible number of neighbors for all fish in a cluster relative to cluster size.

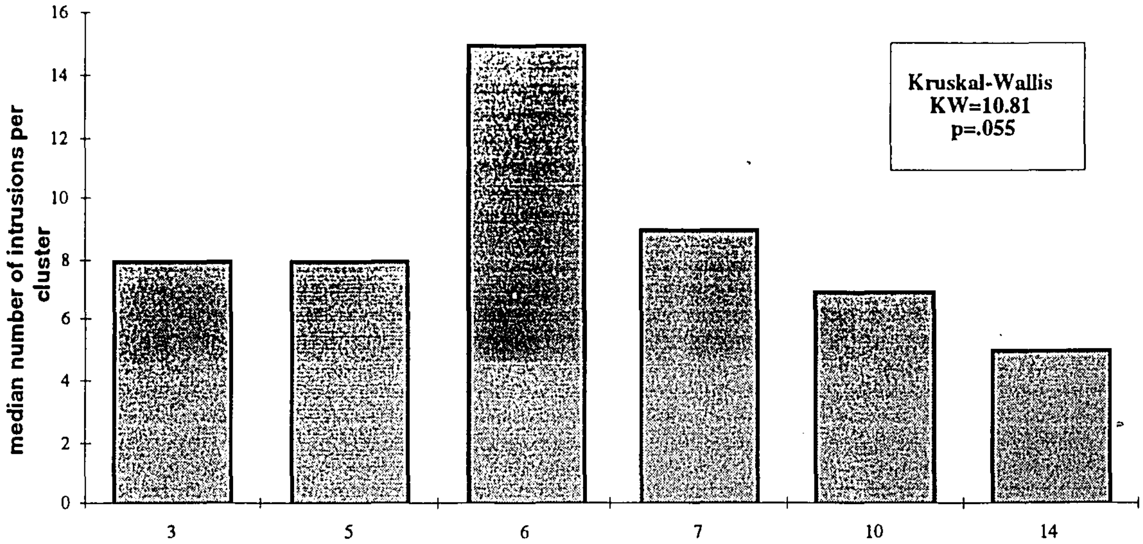

Fig 2. Median number of intrusions observed per cluster relative to cluster size.

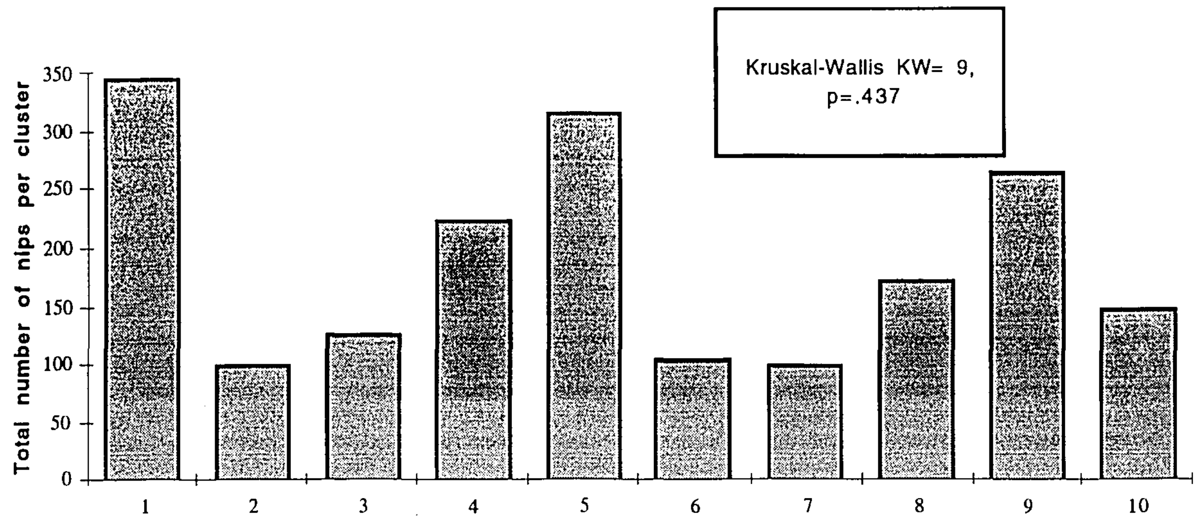

Fig 3. Total number of nips observed by cluster.

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Vitae

I was born on June 3, 1970, in London, UK, daugther of Aida Gonzalez and Ricardo Ludlow. I graduated from Colegio Madrid A.C. (High School) in 1988.

I studied at The National University of Mexico (Universidad Nacional Autonoma de Mexico) from 1988 to 1993, receiving the degree of Biologist. I did my honour s thesis at the Marine laboratory of the Institute of Marine Sciences of the University, on a behavioral study of a coral-reef fish.

I entered the graduate program at Lehigh University in 1993. My professional experience has been mostly doing research at the Marine laboratory in Mexico and at the University of Edinburgh in Scotland, UK.

Upon completion of my Master s degree I intend to pursue a Ph.D. and follow a career in research.

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